

Effects of live and post-mortem shell structures of invasive Pacific oysters and native blue mussels on macrofauna and fish

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ABSTRACT: Blue mussels *Mytilus edulis* and the invasive Pacific oyster *Crassostrea gigas* are both ecosystem engineering species which modify the environment, thus having large effects on associated species. With the introduction of the Pacific oyster, a new biogenic structure has been added to subtidal sediment habitats in Scandinavia. By conducting a field experiment, the effects of live and post-mortem shell structures of *C. gigas* and *M. edulis* on associated infauna, epibenthic fauna and fish on the Swedish west coast were evaluated. Plots with 5 different treatments (live Pacific oysters, oyster shells, live blue mussels, mussel shells and sand control) were constructed on bare sandy sediment at 2 subtidal localities. Epibenthic macrofauna and fish were sampled with a drop trap, and sediment and infauna samples were collected with sediment cores. Live bivalve treatments had significant effects on organic content of the sediment; however, no treatment effects on infauna were found. In contrast, abundance and biomass of epibenthic fauna increased 4 to 8 times and species richness increased in the presence of the bivalves or their shells, compared to the sand control. Epibenthic fauna abundance and biomass was higher in the oyster shell treatment compared to the live bivalve treatments, which in turn had higher abundance and biomass than the mussel shell treatment. In general, the mussel shell treatment favoured small crustaceans, while the oyster shell and live bivalve treatments favoured fish and larger invertebrate species. Based on these results, we conclude that further establishment of the Pacific oyster in Swedish waters will cause large changes to community structure of benthic macrofauna and fish.

KEY WORDS: Non-indigenous species · Ecosystem engineering · Habitat modification · Macroinvertebrates · Infauna · Epibenthic fauna · Sediment community · *Crassostrea gigas* · *Mytilus edulis*

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INTRODUCTION

Blue mussels *Mytilus edulis* and Pacific oysters *Crassostrea gigas* are ecosystem engineers (sensu Jones et al. 1994) with many ecological functions in common, e.g. they are both allogenic and autogenic engineering species (Jones et al. 1994). As allogenic engineers, they modify the sediment condition by adding high loads of organic-enriched particles, thus affecting the organic matter content and oxygen con-

ditions of the sediment (Castel et al. 1989, Commito et al. 2008) and hence the infauna community (Castel et al. 1989, Dittmann 1990). As autogenic engineers, they generate shell structures that constitute an abiotic resource for the associated community, e.g. interstitial-shell spaces as shelter from predators, colonisation substrate for algae and invertebrates and refuge and foraging substrate for many invertebrates and fish (Arve 1960, Newell 1988, Lenihan 1999). Similar autogenic engineering effects have

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also been observed in post-mortem structures of oysters (Guo & Pennings 2012). In addition, being filter-feeding bivalves, they also influence the trophic structure (reviewed by Grabowski & Peterson 2007). By removing plankton from the water column, they promote benthic flora and fauna, and prevent nutrients from entering and staying in lower trophic levels. Moreover, by enhancing the nutrient transfer to benthic invertebrates, the nutrient flux also increases to higher trophic levels such as crabs, demersal fish, and ultimately to predatory fish, many of which are fished commercially. As a consequence, bivalve beds tend to have higher species richness, and higher total abundance or biomass of epifauna (mobile and sessile) and nekton than bare sediment habitats (Hosack 2003, Van Broekhoven 2005, Royer et al. 2006, Kochmann et al. 2008, Troost 2010, Lejart & Hily 2011).

In many aspects, the habitat-modifying effects of blue mussels and Pacific oysters are similar. However, the physical structures of the 2 species are quite different, which may cause differences in autogenic engineering effects of the species: while blue mussels form layered bed structures which are held together with byssal threads, Pacific oysters are found solitary at low population densities and at high densities form solid reef-structures that are cemented together. The 3-dimensional structure, heterogeneity and micro-habitats formed by the 2 species are therefore very different due to the spatial arrangement of shells, degree of shell aggregation, leverage and individual shell traits (i.e. surface area and shell texture) (Gutiérrez et al. 2003). There are also physical differences between live and post-mortem (empty) shell structures of these species. For empty shells, individual shell traits, such as shell volume and aperture width, will influence shell selection by shell-dwellers and determine the space available for shelter and hence the maximum size of the sheltering organisms (Gutiérrez et al. 2003). Thus, for larger mobile species, such as fish and shrimps, the complex structures formed by these 2 bivalves are likely to provide different resources in terms of nesting sites and shelter from predators. In addition, bivalve shell structures may contribute to an increase in organic content of the sediment by increasing sedimentation among the shell residues. Furthermore, the stability of post-mortem structures of the 2 species may differ. The shells of blue mussels are easily disintegrated by wave action, while the solid reef structures formed by the Pacific oysters remain stable for long periods of time (Reise & van Beusekom 2008).

The blue mussel is native to the north Atlantic, while the Pacific oyster, which is native to the Pacific coast of Asia, has been introduced both intentionally (Andrews 1980, Drinkwaard 1999, Ruesink et al. 2005) and unintentionally (Andrews 1980) to most parts of the world (Ruesink et al. 2005). This highly invasive oyster was introduced to Europe in the 1960s and has been found in Sweden since 2006 (Wrange et al. 2010). In Sweden, before 2006, the blue mussel was the dominating ecosystem engineer which added hard structures to shallow subtidal sediment areas. However, since the initial establishment of the Pacific oyster, the number of sites with oysters and the oyster densities have increased dramatically (Wrange et al. 2010). At a few sites, oyster reef structures have been established, although at the majority of sites, oysters still occur as solitary individuals or form small clusters. Thus *C. gigas* has added a range of biogenic structures that is new to the littoral ecosystem in Sweden (Wrange et al. 2010, P. Norling and Å. Strand pers. obs.). In addition, at many places, blue mussel beds have been partly or fully replaced by oysters (P. Norling and Å. Strand pers. obs.), and the oysters are also colonizing areas with mixed and sandy sediments. It is unknown what consequences this change in habitat structure and addition of long-lasting solid biogenic structures (Reise & van Beusekom 2008) will have for the associated communities in these subtidal sediment habitats.

Despite the numerous studies conducted on the role of mussel and oyster beds as habitat for epibenthic fauna and infauna in estuarine and marine systems (e.g. Wells 1961, Castel et al. 1989, Dittmann 1990, Ragnarsson & Raffaelli 1999, Lenihan et al. 2001, Norling & Kautsky 2008), very few studies have included fish assemblages (Breitburg 1999, Posey et al. 1999, Tolley & Volety 2005) and studied effects in subtidal habitats (Norling & Kautsky 2008). In addition, only a few studies have compared the community structure in native bivalve beds to that of alien bivalve beds, such as *C. gigas* beds (Escapa et al. 2004, Kochmann et al. 2008, Markert et al. 2010, Lejart & Hily 2011) and have studied effects of low oyster densities and shell structures (Gou & Pennings 2012, Green & Crowe 2013). To our knowledge, among these latter studies none have included fish assemblages.

The aim of this study was to evaluate and compare the effects of the invasive Pacific oyster and native blue mussel on associated macrofauna and fish in subtidal sandy habitats. We tested the hypothesis that the allogenic engineering effects of blue mussels and Pacific oysters are similar while the autogenic

engineering effects of the 2 species are different, causing an overall change in community structure of macrofauna and fish when going from a native blue mussel habitat to a Pacific oyster-dominated habitat, and from live bivalve beds to post-mortem structures. The allogenic engineering effects of the bivalves were measured on associated infauna, while the autogenic engineering effects were measured on associated benthic epifauna and fish. Species richness, composition, abundance and biomass of infauna, epibenthic fauna and fish in constructed live *C. gigas* plots and plots with shells from dead Pacific oysters were contrasted against that of live *M. edulis* plots and plots with shells from dead blue mussels to study the differences in community structure. In addition, the associated community of bivalve plots was compared to that of bare sandy sediment habitats, which was used as a control treatment.

MATERIALS AND METHODS

To evaluate the ecosystem engineering effects of Pacific oysters and blue mussels on associated communities of infauna, epibenthic fauna and fish, a 3 mo field experiment was conducted.

Experimental setup

Live individuals and empty shells of *Mytilus edulis* were collected from Rossö harbour (58° 51.283' N, 11° 10.475' E) and live individuals and empty shells of *Crassostrea gigas* were collected from Krokesundet (58° 51.691' N, 11° 10.437' E) in the Tjärnö area, Swedish west coast. The collected bivalves were sorted based on the respective approximate size at 2 yr of age, 6 to 10 cm for oysters and 5 to 6 cm for mussels, and were all cleaned from attached epiphytes and epifauna. Only individual oysters (no clusters) were used for the experiment.

The experiment was performed in the beginning of June 2010 at 2 sites, Timmerholmarna (58° 50.103' N, 11° 9.196' E) south of Tjärnö and Svaneskär (58° 55.422' N, 11° 7.263' E) north of Tjärnö close to Strömstad (hereafter called southern site and northern site, respectively). Both sites were sheltered areas with sandy sediment, and were assumed to be suitable habitats for both Pacific oysters and blue mussels (hereafter called oysters and mussels) as both species were previously found at the selected sites but had been killed during the previous winter. The oysters and mussels were placed in different treatment plots:

'Oyster' (O), 'Oyster shell' (OS), 'Mussels' (M), 'Mussel shell' (MS) and 'Control' (C). At each site, 3 replicates of each treatment were placed randomly at approx. 45 cm mean low water (MLW) depth, thus the plots were always under water since the tidal range is very small (approx. 20 cm). Each replicate constituted of a 0.7 × 0.7 m square in which the same number of live animals or shells were placed with a coverage of 100%. The structure of the beds was formed to resemble that of natural blue mussel beds and Pacific oyster beds that had not yet reached high enough densities to form reef structures. Each corner of the squares was marked by a green plastic rod. The squares were placed 1 m apart.

Field sampling

At the end of August, each plot was sampled using a Pihl-Rosenberg drop trap (Pihl & Rosenberg 1982) with a sampling volume of 0.7 × 0.7 × 0.7 m using the same methods as Nohrén et al. (2009). The trap was carefully carried on a 5 m long stick and was then quickly dropped over the experimental plot, guided by the plastic rods that had previously been placed at the experimental plot corners. After the trap had been dropped, 2 sediment cores (Ø 10 cm) were used to sample infauna (10 cm sediment was sampled) and 1 sediment core (Ø 2.6 cm) was used to collect sediment for analysis of organic content (1 cm top sediment was sampled). Thereafter, all oysters, mussels or shells were removed from the plot and placed into a bucket to be checked for accompanying macrofauna before they were put aside. Then the area within the trap was carefully gone through with a net (1 mm mesh size) to catch all epibenthic macrofauna in the trap. The trap was netted until 5 repeated nettings with no catch were obtained. For each sample, all large animals were immediately separated from the gravel residues obtained during netting and both the large animals and gravel residues were put in an ice-filled cooler for transportation to the research facility. At the research facility, the infauna samples were sieved using a 1 mm mesh, rinsed with tap water and put in 4% formalin for later species determination. The larger animals from the epibenthic fauna samples were put in a freezer (-25°C) and the remainder of each sample was separated into 3 fractions: >10 mm, 1–10 mm, and a floating fraction (matter and animals floating when the gravel fraction was stirred in a big plastic container filled with water). All sample fractions were then frozen for later sorting and analysis.

Sample treatment

For determination of organic content of the sediment, the top 1 cm of each sediment core was collected and dried for 12 h at 70°C to constant weight. Thereafter it was burned at 500°C for 6 h and weighed again. Sediment organic content was then calculated as percent organic content of the dried sample. Species identification of the infauna was conducted using a dissecting microscope. All macrofauna was identified to lowest possible taxa, except for the Oligochaeta that was only identified to subclass, and number of individuals of each species was counted. Infauna biomass was not measured.

All epibenthic fauna from the frozen fractions obtained during sampling (large animals, floating fraction, 1–10 mm gravel and >10 mm gravel) were sorted, determined to species level (when possible), measured and counted. Most of the polychaetes were damaged and fragmented and therefore head counted and only determined to family level, i.e. Nereididae, Polynoidae and Spionidae. For the amphipods, the families Gammaridae, Talitridae and Aoridae were all merged into one group after subsampling due to the extremely large number of individuals. A similar procedure was used for the species within the genus Littorinidae and Palaeomonidae/Alpheidae. Newly recruited blue mussels were also included in the analysis. For the genus *Pomatoschistus*, many individuals were impossible to identify to species level, thus in all abundance and biomass analysis, the genus was used instead of species.

For some species, equations describing ash free dry weight (AFDW, mg) in relation to length of the animal were available from reference literature (see Table S2 in the Supplement at www.int-res.com/articles/suppl/m518p123_supp.pdf). For these species, lengths of the animals were recorded according to the methods described in the literature (mostly the carapace length or total length), and biomass was calculated using the existing equations. For some species, equations were missing and were therefore developed in this study. The individuals of these species were dried at 105°C for 24 h to constant weight and then burned at 500°C for 6 h. The AFDW of the individuals was then calculated by subtracting the burnt weight (ash content) from the initial dry weight of the individuals. For all species with a total number of 6 or more individuals, equations describing the length–AFDW relationship were developed using the pre-registered individual length data (see Table S2 for details) and AFDW of

all individuals for the respective species. Due to the fragmented state of many of the Polychaeta, only biomass as AFDW was determined and no equation was created.

Statistical methods

During sampling it was noted that some of the mussel shell treatments (MS) had been impacted by waves, lowering the total area cover of the treatment to 25, 40 and 75% in 3 of the plots (the remaining 3 plots had still 100% cover of blue mussel shells). All MS treatment replicates were, however, included in the data analysis. SPSS Statistics 19 (IBM) was used for all factorial analysis. Effects of site (northern and southern) and treatment (oysters, oyster shells, mussels, mussels shells, control) on the variables (organic content of the sediment; infauna: species richness and total abundance; epibenthic fauna [including fish]: species richness, total abundance and total biomass) were tested at the 0.05 significance level by univariate general linear models (GLM) after Levene's test of equality of error variances was conducted and residual plots were explored. Site was treated as a random factor and treatment as a fixed factor. If no significant interactions ($p > 0.25$) were found, the residual and interaction terms were pooled to obtain a stronger test for main effects in accordance with Underwood (1997). Tukey HSD was used as post-hoc test. In the case of non-homogenous sample variations, Tamhane's T2 test was used for pair-wise comparisons and in addition, to assess the robustness of conclusions from parametric tests, a combination of non-parametric tests (Kruskal-Wallis for main effects and Mann-Whitney U -tests for pair-wise comparisons) were used. Sediment data were arcsine-square-root-transformed and abundance and biomass data were 4th-root-transformed before analysis. All non-parametric tests were performed on untransformed data.

Differences in species composition (hereafter SC), species abundance (hereafter SA), and species biomass (hereafter SB) of epibenthic fauna (including fish), and SC and SA of infauna were analysed using multivariate methods (Primer 6.1.13 and PERMANOVA+ 1.0.3, Primer-E). Patterns of SC, SA and SB were analysed using Bray-Curtis dissimilarities with SC being presence/absence-transformed and SA and SB being 4th-root-transformed before analysis. The class Polychaeta was excluded from the abundance analysis in the epibenthic fauna analysis as fragmentation of the individuals did not allow for the accurate

determination of actual numbers of individuals in each sample. All variables were analysed with site (northern and southern) as random factor and treatment (oysters, oyster shells, mussels, mussel shells, control) as fixed factor. If no significant interactions ($p > 0.25$) were found, the residual and interaction terms were pooled to obtain a stronger test for main effects. PERMANOVA pairwise comparisons between treatment categories were used as post-hoc test. The Pearson product-moment correlation coefficient obtained from canonical analysis on the principal coordinates (CAP) was used to identify species, which were driving observed differences among treatments.

RESULTS

Allogenic engineering effects on organic content of sediment and infauna

Despite transformation, unequal variances were obtained for the sediment data and analyses were performed using non parametric tests. The presence of live mussels (M) (organic content, mean \pm SD: $3.0 \pm 1.4\%$) and oysters (O) ($2.7 \pm 0.3\%$) were found to increase the organic content of the sediment in comparison to bare sediment (C) ($1.4 \pm 0.3\%$), as did the oyster shell (OS) ($1.9 \pm 0.3\%$) treatment (Kruskal-Wallis test, $df = 4$, $p = 0.006$; Mann-Whitney *U*-test, $p < 0.05$; Fig. 1), but not the mussel shell (MS) ($2.0 \pm 0.9\%$) treatment (Mann-Whitney *U*-test, $p = 0.147$). In contrast, organic content of the sediment did not differ significantly between live oysters and mussels (Mann-Whitney *U*-test, $p = 0.810$). Sediment organic content was higher in the oyster treatment compared to the oyster shell treatment (Mann-Whitney *U*-test, $p < 0.05$), and very nearly significantly higher than in the mussel shell treatment (Mann-Whitney *U*-test, $p < 0.054$; Fig. 1). A similar trend was noted for the mussel treatment compared to the shell treatments (MS and OS), although the differences were not significant (Mann-Whitney *U*-test, $p = 0.108$ and 0.092 for M vs. MS and M vs. OS, respectively).

No allogenic engineering effects of the bivalve treatments, in terms of differences in species richness (GLM, $F_{4,24} = 0.56$, $p = 0.697$) and total abundance (GLM, $F_{4,24} = 1.5$, $p = 0.248$) of infauna compared to the control, were found. However, a general qualitative trend of decreasing infauna abundance in the bivalve treatments compared to the control was observed (Fig. 2, Table S1 in the Supplement). In contrast, multivariate statistical analysis revealed that

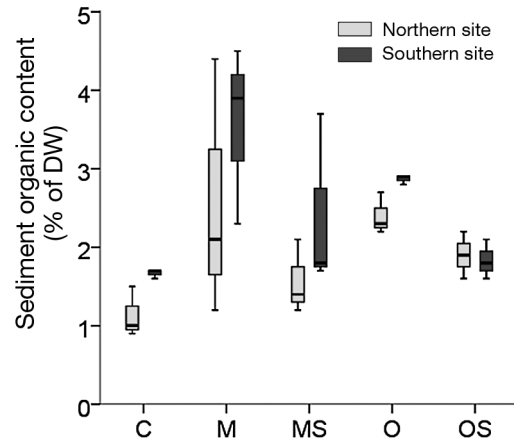


Fig. 1. Sediment organic content as % organic content of sample dry weight (DW) from different treatment plots: Pacific oysters (O), oyster shells (OS), blue mussels (M), mussel shells (MS) and control (C) at shallow, sub-tidal, sandy areas at the Swedish west coast. Boxes represent quartiles, the thick line within boxes represents the median, the whiskers show non-outlier range

there were significant differences in infauna SC and SA between sites (PERMANOVA, Table 1). Due to the significant interaction between sites and treatments ($p < 0.25$) for both SC and SA, tests were also done at both sites separately in order to explore potential differences among treatments. No significant effects of the treatments were, however, found at either site (PERMANOVA, $p > 0.05$).

Autogenic engineering effects on epibenthic fauna: factorial analyses

Autogenic engineering effects of live bivalves and post-mortem structures on epibenthic fauna were found in terms of increased total abundance and total biomass (Fig. 3, GLM, Table 2 and in addition, for

Table 1. PERMANOVA analysis of effects of site (northern and southern) and treatment (Pacific oysters, oyster shells, blue mussels, mussel shells and control) on infauna species composition and species abundance at the Swedish west coast. Significant values ($p < 0.05$) in bold

Source	df	Species composition		Species abundance	
		MS	p	MS	p
Site	1	8345	0.001	6989	0.001
Treatment	4	688	0.646	665	0.576
Site \times Treatment	4	811	0.056	737	0.087
Residual	20	496		512	

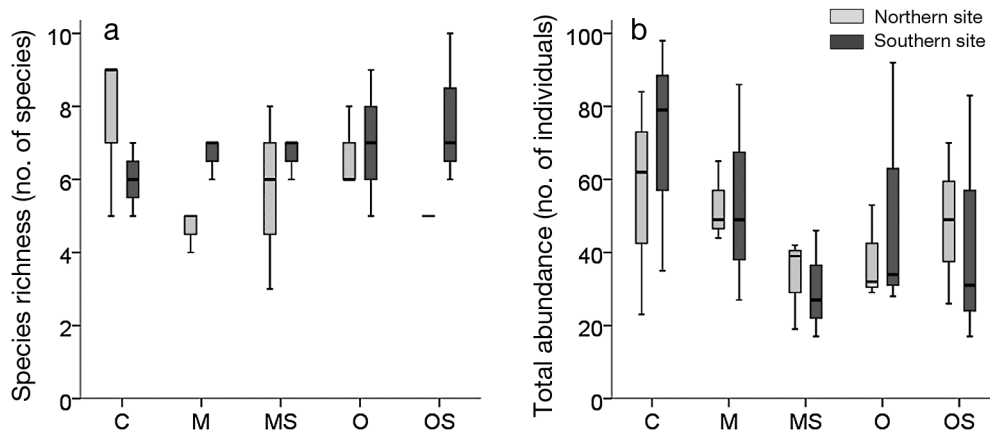


Fig. 2. Species richness and total abundance of infauna in core samples (0.0075 m²) from different treatment plots: Pacific oysters (O), oyster shells (OS), blue mussels (M), mussel shells (MS) and control (C). Box plots as in Fig. 1

biomass data, Kruskal-Wallis test, $df = 4$, $p < 0.001$), and were higher in all treatments compared to the control (total abundance: Tukey HSD post-hoc, $p < 0.05$, species biomass: Tamhane's T2 test and Mann-Whitney U -test, $p < 0.05$; Fig. 3). However, total

abundance and total biomass did not differ between mussels and oysters, nor did the total abundance and total biomass in live bivalve treatments differ from that of post-mortem structures (abundance data Tukey HSD post-hoc, biomass data Tamhane's T2

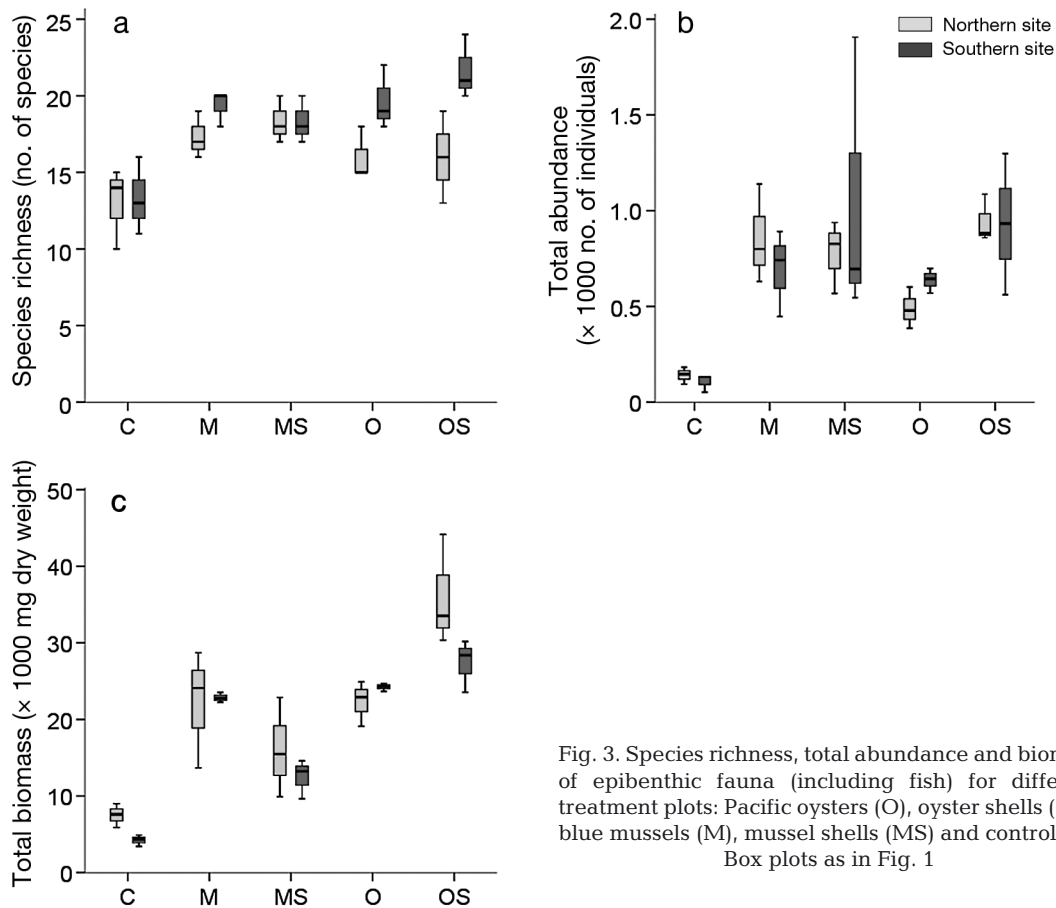


Fig. 3. Species richness, total abundance and biomass of epibenthic fauna (including fish) for different treatment plots: Pacific oysters (O), oyster shells (OS), blue mussels (M), mussel shells (MS) and control (C). Box plots as in Fig. 1

test, $p > 0.05$; Fig. 3). Due to the non-homogenous variances observed in the biomass data (Levene's test, $F_{4,25} = 3.3$, $p = 0.028$), non-parametric pair-wise comparisons were also performed, revealing significant differences between live and post-mortem structures that were not visible in the parametric tests. Both mussel and oyster treatments had higher epibenthic fauna biomass compared to the mussel shell treatment, but lower biomass compared to the oyster shell treatment (Mann-Whitney U -test, $p < 0.05$, Fig. 3), and as a consequence, the oyster shell treatment also had significantly higher biomass compared to the mussel shell treatment (Mann-Whitney U -test, $p < 0.05$; Fig. 3). However, biomass of epibenthic fauna in the mussel and oyster treatments was similar (Mann-Whitney U -test, $p > 0.05$; Fig. 3). In addition, no significant effect of treatment on species richness was detected, nor of site on any of the 3 variables, although a trend for higher species richness in live bivalves and shell structures were noted (GLM, Table 2).

Table 2. Generalized linear model (GLM) analysis of effects of site (northern and southern site) and treatment (Pacific oysters, oyster shells, blue mussels, mussel shells and control) on species richness, total abundance and total biomass of epibenthic fauna. Significant values ($p < 0.05$) in bold

Source	df	Species richness		Species abundance		Species biomass	
		MS	p	MS	p	MS	p
Site	1	40.1	0.108	<0.01 ^a	0.979 ^a	0.2 ^a	0.807 ^a
Treatment	4	32.8	0.092	5.0 ^a	<0.001^a	30.3 ^a	<0.001^a
Site × Treatment	4	8.4	0.135	0.1	0.655	2.4	0.494
Residual	20	4.2		0.2		2.7	

^aBased on the analysis performed after the interaction term had been pooled; $df_{\text{residual}} = 24$

Table 3. PERMANOVA analysis of site (northern and southern site) and treatment (Pacific oysters, oyster shells, blue mussels, mussel shells and control) on species composition, abundance and biomass of epibenthic fauna. Significant values ($p < 0.05$) in bold

Source	df	Species composition		Species abundance		Species biomass	
		MS	p	MS	p	MS	p
Site	1	2028	0.001^a	2880 ^a	0.001^a	3765	0.001
Treatment	4	1216	0.001^a	1599 ^a	0.001^a	1745	0.020
Site × Treatment	4	449	0.374	293	0.164	494	0.011
Residual	20	412		220		269	

^aBased on the analysis performed after the interaction term had been pooled; $df_{\text{residual}} = 24$

Autogenic engineering effects on epibenthic fauna: multivariate analyses

Multivariate analyses revealed that there were significant differences among sites and treatments on the SC, SA and SB of epibenthic fauna (PERMANOVA, Table 3). The observed p -value for the interaction term in the SA analysis was slightly lower ($p = 0.164$, Table 3) than recommended ($p > 0.25$) for pooling the residual and interaction term. However, to reduce the risk of making type II errors, and to make possible pair-wise comparison of the different treatments (without pooling, the number of replicates are 3, alternatively the number of permutations are 10, making pair-wise comparisons impossible), the residual and interaction terms were pooled. This decision is further strengthened by the estimates of components of variation for the factors and interaction term (2880, 1599 and 293 for the factors Site, Treatment and Site × Treatment, respectively, before pooling), demonstrating the minor contribution to the variance by the interaction term.

PERMANOVA pair-wise comparisons among treatments revealed that epibenthic fauna SC, SA and SB in the bivalve treatments and in the post-mortem structures were all different from the control treatment (PERMANOVA, $p < 0.05$; Table 4). SC, SA and SB did not differ between the 2 species of live bivalves (Table 4), but SC and SA were significantly different between live and post-mortem structures of mussels (PERMANOVA, $p < 0.05$; Table 4). In addition, the SC, SA and SB of plots containing post-mortem structures of mussels and oysters differed significantly (PERMANOVA, $p < 0.05$; Table 4).

CAP analysis revealed that the control treatment was separated from the other treatments along the first axis for both the SC (CAP, correlation value = 0.84; Fig. 4a) and SA (CAP1, correlation value = 0.93) data. Additionally, for SA, there was also a significant correlation with the second axis (CAP2, correlation value = 0.73), which appear to represent a difference in composition between post-mortem mussels compared to all other treatments (Fig. 4b). Further inspection of Pearson correlations

Table 4. PERMANOVA pair-wise test of effects of treatment (T1, T2; Pacific oysters [O], oyster shells [OS], blue mussels [M], mussel shells [MS] and control [C]) on species composition, abundance and biomass of epibenthic fauna. t = test statistics t -values, $p(\text{perm})$ = significance of the permutation test, $p(\text{MC})$ = significance of the Monte Carlo test; bold indicates significant ($p < 0.05$) values

Test		Species composition ^a		Abundance ^a		Biomass north ^b			Biomass south ^b		
T1	T2	t	$p(\text{perm})$	t	$p(\text{perm})$	t	$p(\text{perm})$	$p(\text{MC})$	t	$p(\text{perm})$	$p(\text{MC})$
OS	MS	1.5	0.034	2.0	0.006	1.9	0.119	0.057	2.1	0.111	0.031
OS	C	2.0	0.006	3.4	0.005	2.9	0.112	0.006	2.9	0.085	0.005
OS	O	0.8	0.714	1.7	0.007	1.9	0.096	0.048	1.6	0.107	0.079
OS	M	0.9	0.625	1.3	0.086	1.1	0.386	0.318	1.5	0.097	0.155
MS	C	2.1	0.002	3.5	0.003	2.1	0.114	0.036	2.7	0.099	0.015
MS	O	1.5	0.030	1.9	0.004	1.2	0.331	0.246	1.5	0.093	0.120
MS	M	1.8	0.007	2.1	0.003	1.2	0.291	0.270	1.9	0.093	0.065
C	O	1.9	0.003	2.9	0.004	2.6	0.102	0.019	2.4	0.125	0.023
C	M	2.2	0.001	3.3	0.002	2.4	0.085	0.025	2.7	0.099	0.015
O	M	0.9	0.638	1.5	0.053	1.2	0.188	0.272	1.1	0.312	0.324

^aPairwise comparisons performed on data for which the residual and interaction term were pooled and treatment was used as factor

^bPairwise comparisons performed using the interaction term as factor

revealed that the shrimp *Crangon crangon* (both SC and SA data) and *Limanda limanda* (SA data) were found more frequently in control plots compared to the other treatments ($n = 30$, $R_{\text{crit}} \leq -0.36$). The main species favoured by the presence of bivalves and post-mortem shell structures coincided to a great extent between the 2 datasets and were; the polychaete family Polynoidae (SC), several decapods (*Palaemon elegans* [SC and SA], *Athanas nitescens* [SC], *Pagurus bernhardus* [SC] and *Carcinus maenas* [SA]) and fish species (*Gobiusculus flavescens* [SC and SA], *Pholis gunnellus* [SC and SA], *Gobius niger* [SA] and *Myoxocephalus scorpius* [SA]), molluscs (*Leptochiton asellus* [SC], *Tonicella* sp. [SC and SA], *Littorina* sp. [SA] and *M. edulis* juvenile [SA]), as well as amphipods (Corophiidae [SC and SA] and Gammaridae/Talitridae/Aoridae [SA]), and the starfish *Asterias rubens* (SC and SA) ($n = 30$, $R_{\text{crit}} \geq 0.36$).

To facilitate interpretation of the interaction found for the SB data, CAP analyses were performed for the 2 sites separately. For the northern site, 3 CAP axes were found to describe the differences in SB between treatments well (CAP1, correlation value = 0.99; CAP2, correlation value = 0.96 and CAP3, correlation value = 0.87, Fig. 5a), while for the southern site, one axis was found to describe the differences in SB between treatments well (CAP1, correlation value = 0.97; Fig. 5b). At the northern site, the labrid fish *Symphodus melops* was dominant in terms of biomass in the control treatment ($n = 15$, $R_{\text{crit}} \leq -0.51$) and was found to associate with loosely lying *Fucus vesiculosus* specimens, whereas *C. crangon* was the dominant

species at the southern control site ($n = 15$, $R_{\text{crit}} \leq -0.51$). As in the SA data, species with higher biomass in the bivalve treatments and in the presence of shell structures were *Littorina* sp. (northern site), 2 decapods (Palaemonidae/Alpheidae and *C. maenas*, both sites), Gammaridae/Talitridae/Aoridae (northern site), 4 molluscs (*Littorina* sp., *Nassarius nitidus*, *Leptochiton* sp. and *M. edulis* juveniles; southern site), the polychaete family Polynoidae (southern site), and the starfish *A. rubens* (both sites) ($n = 15$, $R_{\text{crit}} \geq 0.51$). In addition, at the southern site, several fish species (*M. scorpius*, *P. gunnellus*, *G. flavescens*, and *G. niger*) had higher biomass in both the bivalve and the shell structure treatments ($n = 15$, $R_{\text{crit}} \geq 0.51$).

The observed differences in SC, SA and SB between the post-mortem structures were found to be explained by occurrence of *Jaera* sp. and *C. crangon* (SC, SA and SB) in the mussel shell treatment, together with *Idotea baltica* (SB), *Corophium* sp. (SC) and *Littorina saxatilis* (SC) in mussel shells, while *P. gunnellus* (SC and BM), *Pomatoschistus* sp. (SC), *G. flavescens* (SB), *Macropodia rostrata* (SC), Chironomidae (SC), *Littorina* sp. (SB) and Asteriidae (SB) were prominent in the oyster shell treatment. Post-mortem structures of mussels differed from live bivalves by the presence of Corophiidae (SC and SA), *Jaera* sp. (SC), *C. crangon* (SC), *Lepidochitona cinerea* (SC), *Pomatoschistus* sp. (SA) and *M. edulis* juveniles (SA) in mussel shells. Sites with live bivalves favoured *Athanas nitescens* (SC), Palaemonidae/Alpheidae (SA), *M. rostrata* (SC), *M. scorpius* (SC), *G. niger* (SA) and Asteriidae (SA).

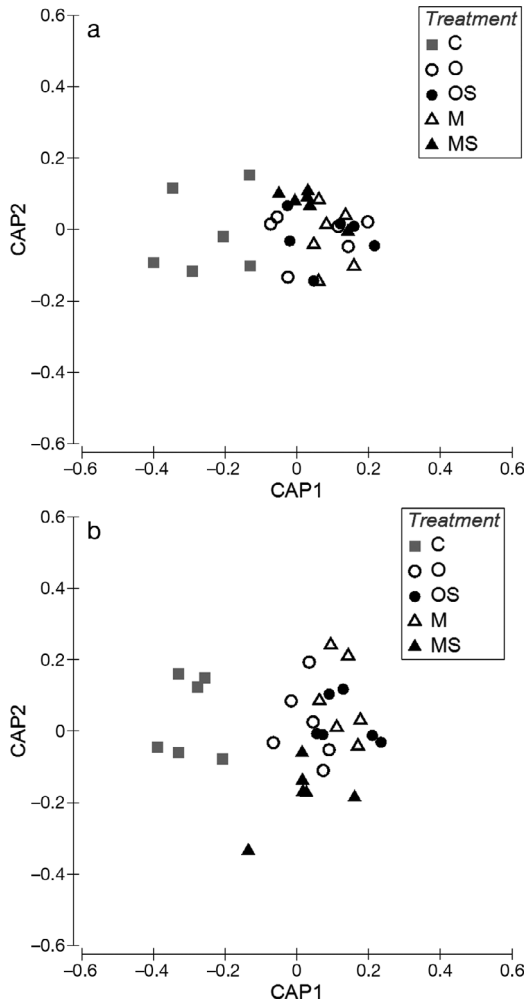


Fig. 4. Canonical analysis on the principal coordinates (CAP) analysis of the effect of different treatments: Pacific oysters (O), oyster shells (OS), blue mussels (M), mussel shells (MS) and control (C) on (a) epibenthic fauna species composition and (b) species abundance

To summarize the PERMANOVA pair-wise comparisons and CAP analysis results, clear differences in SC, SA and SB were seen between the control and the other treatments. Primarily, *C. crangon* and *L. limanda* were favoured by the control, while many different organism groups such as decapods, molluscs, amphipods and several fish species were favoured by any added structure. There were no differences in SC, SA or SB between live oysters or mussels, but all 3 variables differed significantly between post-mortem structures of the bivalve species, and SC and SA in post-mortem structures of mussels differed from that of live bivalves. Small crustaceans were found to reside in the mussel shell treatment while oyster shells and live bivalves favoured larger fish species and starfish.

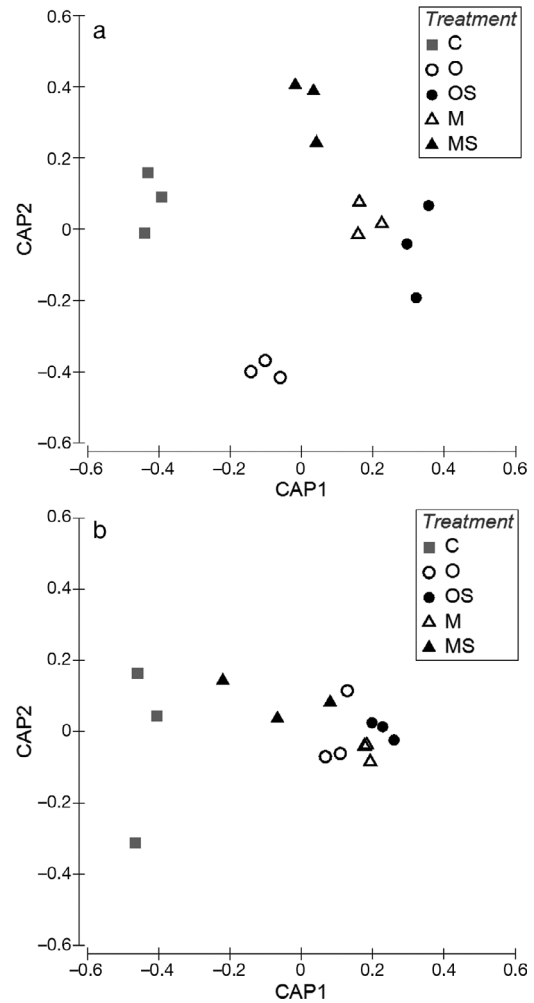


Fig. 5. Canonical analysis on the principal coordinates (CAP) analysis of the effect of different treatments: Pacific oysters (O), oyster shells (OS), blue mussels (M), mussel shells (MS) and control (C) on epibenthic fauna species biomass at the (a) northern and (b) southern site

Autogenic engineering effects on the fish community

Occurrence of fish individuals and species were very uneven between the 2 sites. Of a total of 12 species, 11 were found at the southern site while only 8 species were found at the northern site. The most abundant taxa were *M. scorpius*, *G. niger*, and the genus *Pomatoschistus*. At the northern site the genus *Pomatoschistus* constituted 86% of the total fish recorded, with only 14 other individuals from 5 species. The corresponding percent for the southern site was 27%, with 152 individuals from 8 species. This made statistical analysis of the data at the northern site very difficult. Therefore, the 2 sites were analysed separately. At the northern site, no significant

Table 5. Generalized linear model (GLM) analysis of effects treatment (Pacific oysters, oyster shells, blue mussels, mussel shells and control) on fish species richness, total abundance and total biomass at the southern site. Significant values ($p < 0.05$) in bold

	df	Fish species richness		Fish total abundance		Fish total biomass	
		MS	p	MS	p	MS	p
Treatment	4	10.5	0.001	0.18	0.018	7.2	<0.001
Residual	10	0.9		0.04		0.5	

effects of treatment were discovered (GLM, $df = 4$ and 10 for treatment and the residual, respectively, $MS_{\text{species richness}} = 1.7$ and 0.7 , $MS_{\text{total abundance}} = 0.5$ and 0.2 and $MS_{\text{total biomass}} = 4.2$ and 2.1 for treatment and the residual, respectively, $p > 0.05$). At the southern

Table 6. Tukeys t -test post hoc for species richness, total abundance and total biomass of fish between treatments (Pacific oysters [O], oyster shells [OS], blue mussels [M], mussel shells [MS] and control [C]) at the southern site. Significant values ($p < 0.05$) in bold

Test	T1	T2	Species richness	Total abundance	Total south biomass
			p	p	p
C	M		0.023	0.162	0.026
C	MS		0.910	0.530	0.998
C	O		0.286	0.361	0.244
C	OS		0.001	0.009	0.001
M	MS		0.084	0.882	0.040
M	O		0.480	0.974	0.598
M	OS		0.286	0.397	0.151
MS	O		0.715	0.997	0.352
MS	OS		0.003	0.110	0.001
O	OS		0.023	0.181	0.016

site, species richness, abundance and biomass of fish were all significantly affected by treatment (GLM, Table 5).

At the southern site, in general, fish species richness, total abundance and total biomass were lowest in the control and mussel shell treatments and highest in the oyster shell treatment, with live bivalve treatments in between (Table 6, Fig. 6). Post-mortem shell structures of oysters thus had a strong positive effect on species

richness, abundance and total biomass of fish, which was not found in the mussel shell treatment (Table 6). Live bivalves had similar structuring abilities on fish species richness, total abundance and total biomass. Post-mortem structures of Pacific oysters and mussels thus demonstrated different autogenic engineering effects on fish in relation to each other, and also in comparison to live bivalves.

To further evaluate what habitat was preferred by different fish species, factorial analysis were performed on the abundance and biomass data for all fish species from the southern site with more than 5 individuals in total. The resulting species were *G. niger*, *P. gunnellus*, *Pomatochistus* spp., *M. scorpius* and *G. flavescens* (Fig. 7), which all displayed preferences for different habitats (Fig. 7). Due to the large sample variances, non-parametric tests were performed to evaluate differences in abundance and biomass between treatments. Three of the species, *M. scorpius*, *G. flavescens* and *P. gunnellus*, were significantly affected by treatment (Kruskal-Wallis test, $df = 4$, $p > 0.05$; Table 7). In general, adding structural complexity increased abundance and biomass of fish (Mann-Whitney U -test, $p \leq 0.05$;

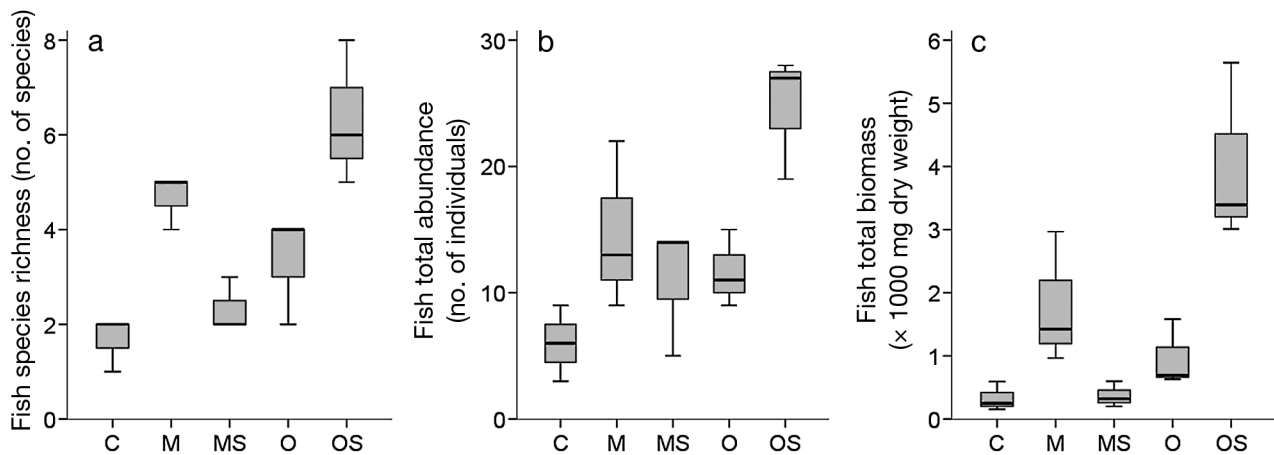


Fig. 6. Species richness, total abundance and biomass of fish in different treatment plots: Pacific oysters (O), oyster shells (OS), blue mussels (M), mussel shells (MS) and control (C) at the southern site. Boxes represent quartiles, the thick line within boxes represents the median, and the whiskers show non-outlier range

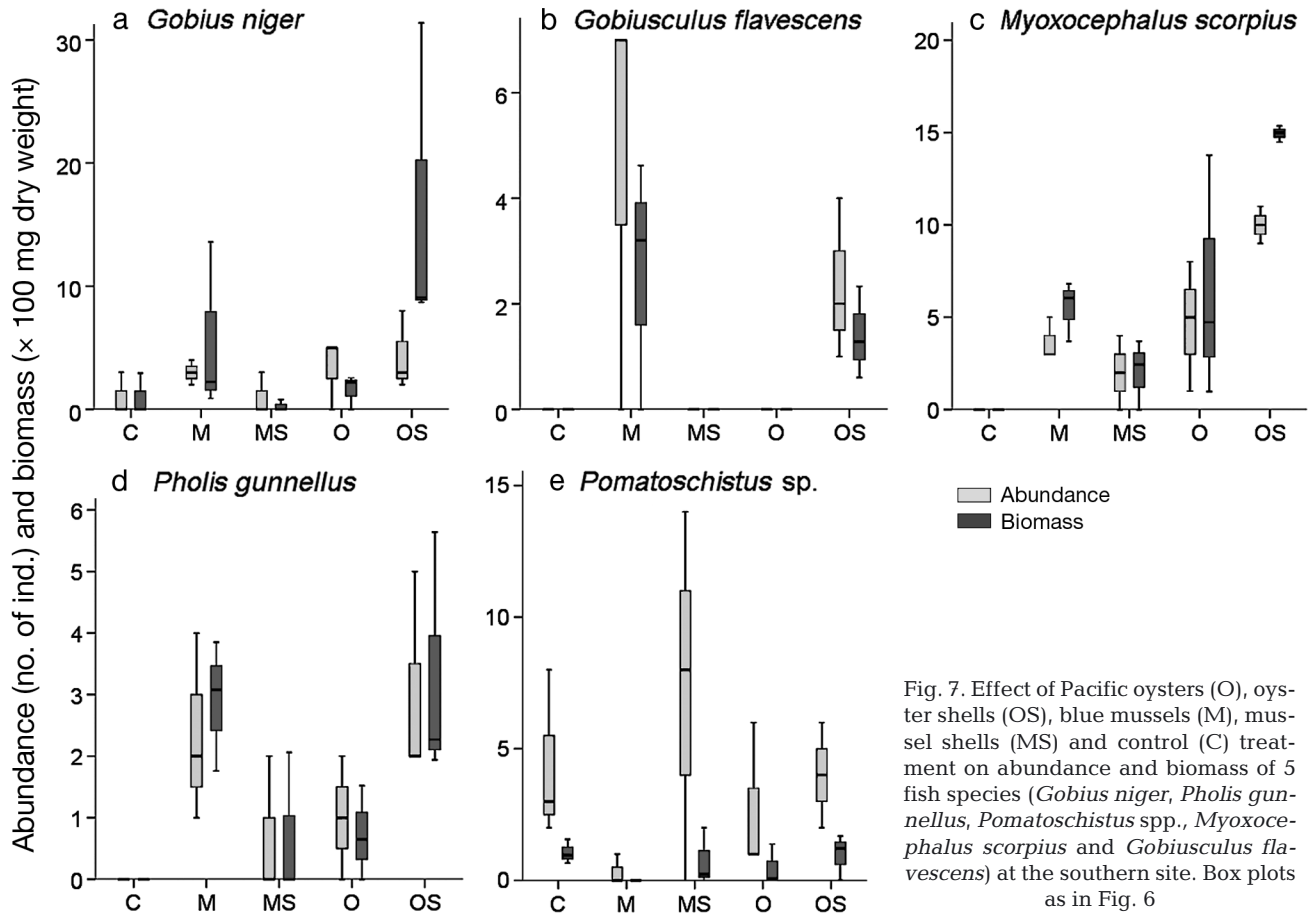


Fig. 7. Effect of Pacific oysters (O), oyster shells (OS), blue mussels (M), mussel shells (MS) and control (C) treatment on abundance and biomass of 5 fish species (*Gobius niger*, *Pholis gunnellus*, *Pomatoschistus* spp., *Myoxocephalus scorpius* and *Gobiussculus flavescens*) at the southern site. Box plots as in Fig. 6

Table 7, Fig. 7). Abundance and biomass of fish in live bivalve treatments did not differ except for *P. gunnellus*, which had higher biomass in the blue mussel compared to the oyster treatment. In accordance with the general analysis of fish abundance and biomass, the oyster shell treatment had significantly higher abundance and/or biomass of 3 different fish species (*M. scorpius*, *G. flavescens* and *P. gunnellus*) in comparison to the live oyster treatment, and for 1 species (*M. scorpius*), also in comparison to live blue mussel treatment. In addition, for 2 species (*M. scorpius* and *G. flavescens*) the oyster shell treatment also had significantly higher abundance and biomass in comparison to the mussel shell treatment (Table 7, Fig. 7).

Table 7. Effects of treatment on abundance (ind; number of individuals) and biomass (Bio; mg DW) and for significant ($p < 0.05$, in bold) main effects, pair-wise comparisons of treatment categories treatments (T1, T2; Pacific oysters [O], oyster shells [OS], blue mussels [M], mussel shells [MS] and control [C]) on 5 different fish species (*Gobius niger*, *Pholis gunnellus*, *Pomatoschistus* spp., *Myoxocephalus scorpius* and *Gobiussculus flavescens*) at the southern site. Because no significant effect of treatment on *G. niger* (Ind. = 0.362, Bio = 0.074) and *Pomatoschistus* spp. (Ind. = 0.224, Bio = 0.226) was observed, no pair-wise testing was done

	<i>P. gunnellus</i>		<i>M. scorpius</i>		<i>G. flavescens</i>	
	Ind.	Bio.	Ind.	Bio.	Ind.	Bio.
Overall effect:	0.072	0.041	0.025	0.020	0.040	0.041
T1 T2						
C M		0.037	0.034	0.037	0.114	0.121
C MS		0.317	0.121	0.121	1.000	1.000
C O		0.121	0.037	0.037	1.000	1.000
C OS		0.037	0.037	0.037	0.037	0.037
M MS		0.121	0.268	0.077	0.114	0.121
M O		0.050	0.653	0.827	0.114	0.121
M OS		0.827	0.046	0.050	0.507	0.513
MS O		0.817	0.275	0.275	1.000	1.000
MS OS		0.121	0.050	0.050	0.037	0.037
O OS		0.050	0.050	0.050	0.037	0.037

DISCUSSION

In this study, the ecosystem engineering effects of live and post-mortem shell structures (empty shells) of the invasive Pacific oyster and native blue mussels on associated species, including fish assemblages, were evaluated in a subtidal sandy sediment habitat. In accordance with the proposed hypothesis, the allogenic engineering effect of Pacific oysters and blue mussels was found to be similar. Furthermore, both Pacific oysters and blue mussels, as well as the post-mortem structures of the species, increased epibenthic species richness, total abundance and biomass compared to the sand control, indicating the importance of both species' autogenic engineering contribution to the community. No differences in epibenthic community structure was, however, found between live Pacific oysters and blue mussels, but the post-mortem structures of the 2 species were found to have different structuring effects: fish species were positively affected by the presence of oyster shells, and small crustaceans were positively affected by the presence of blue mussel shells.

Effects of bivalves on organic content of sediment and infauna

Both live Pacific oysters and blue mussels, and post-mortem structures of oysters, significantly increased the organic content of the sediment, although the enrichment effect was more pronounced in the live bivalve treatments (with a doubling of the organic content compared to the control treatment). Pacific oysters and blue mussels enrich the sediment by excreting high amounts of organic-rich particles. In addition, the heterogenic structures formed by the shells of Pacific oysters and live bivalves also enhance trapping of organic-enriched particles. This combination of autogenic and allogenic engineering effects explains why the organic content of the sediment of both live and empty shells of oyster treatments was higher compared to the control.

In our study, the background levels of organic content in the control patches were in accordance with what can be expected in the area (Norling & Kautsky 2007, Nohrén et al. 2009). The results show that the allogenic engineering effect of Pacific oysters and blue mussels is strong, and is supported by previous data that shows that there only need to be a few mussels to significantly enrich the sediment (Norling & Kautsky 2007). It has also been shown that mixed blue mussel and Pacific oyster reefs can have large-

scale effects (>100 m), increasing sediment organic matter, silt fraction and decreasing redox potential, which in turn can influence the distribution of benthic species (Van der Zee et al. 2012).

Although sediment modification was detected in this study, no significant effects of the oyster or blue mussel treatments on infauna species richness or abundance were found, even though a trend towards reduced infauna abundance in the bivalve treatments (both alive and empty shells) was noted. This result is in accordance with previous studies, which demonstrated that *Crassostrea gigas* clearly enhance meiofauna abundance but reduce macrofauna densities of infauna communities when compared to adjacent sandbanks (Castel et al. 1989), and that *Mytilus edulis* reduce macroinfauna densities in the mussel beds compared to ambient sandflats (Dittmann 1990). This pattern was attributed to the organic-rich bivalve biodeposits probably favouring meiofauna by increasing the trophic resources, but being detrimental to the macroinfauna by inducing low oxygen concentrations (Castel et al. 1989). In contrast, Markert et al. (2010) and Kochmann et al. (2008) demonstrated higher total abundance of infauna in oyster belts, patches and open spaces of *C. gigas* reefs and *M. edulis* plots and patches compared to bare sediments and sand flats. In addition, whether there are differences in abundance of associated infauna in oyster and blue mussel habitats are unclear. In accordance with our results, Markert et al. (2010) did not find significant differences in infauna abundances between *C. gigas* and *M. edulis* treatments, while Kochmann et al. (2008) found significantly higher total abundance of infauna (when excluding Oligochaeta) in *C. gigas* belts compared to *M. edulis* plots. The inconsistencies in effects on the infauna community of live bivalves and shell structures, and between oyster and mussel, mirrors the importance of specific environmental settings rather than an increase in organic content of the sediment per se. The different results may also be a result of different methodology being used, as well as differences in bivalve densities, organic content of sediment and infauna species composition in the different studies.

Autogenic engineering effects on epibenthic fauna: comparisons to controls

In contrast to the infauna, the epibenthic fauna community was significantly affected by the presence of live bivalves and post-mortem shell structures of bivalves. Adding physical structures and hard substrate

(autogenic engineering) to the sediment habitat had a strong impact on the associated epibenthic fauna communities. Both total abundance and total biomass of epibenthic fauna significantly increased in the presence of live bivalves and empty shells of Pacific oysters and blue mussels. A similar qualitative trend was observed for species richness, although the results were not significant. In addition, species composition differed between treatments, thus despite the number of species in the control and shell areas not being significantly affected by the presence or absence of shells, the species composition was altered. The results of increased total abundance and total biomass of epibenthic fauna species in bivalve treatments compared to the sand control are supported by previous studies (Kochmann et al. 2008, Markert et al. 2010), showing that oysters and mussels are important autogenic engineering species which can control the distribution and abundance of associated species directly by adding physical structure (Gutiérrez et al. 2003, Ruesink et al. 2005, Kochmann et al. 2008). By increasing habitat complexity in terms of substrate surface and 3-dimensional structure of the habitat, the bivalves increase the living space and the number of ecological niches for the organisms living on and/or between the shells (Bell et al. 1991, Sebens 1991).

In the present study, we found significant differences in composition, abundance and biomass of epibenthic fauna species between the bivalve treatments and the sand control. The sand shrimp *Crangon crangon*, common dab *Limanda limanda* and corkwing wrasse *Symphodus melops* were found to be associated with the bare sand control. Both sand shrimp and common dab are known to be closely associated with bare sandy sediments, while corkwing wrasse was associated with drifting algae. More species were found to have higher abundance and biomass in the presence of bivalves (or shells of bivalves) compared to the number of species found in the bare sand environment. The results were very similar between species composition, species abundance and species biomass of epibenthic fauna. Organism groups that benefitted from the shell treatments were arthropods (amphipods and decapods such as *Corophium* sp., *Gammarus* spp., *Palaemon elegans* and *Carcinus maenas*), molluscs (Lepidopleurida, Neotaenioglossa, Neogastropoda and Mytiloidea such as *Leptochiton asselus*, *Littorina littorea*, *Nassarius nitidus* and *M. edulis* juveniles), echinoderms (Asteroidea i.e. *Asterias rubens*) and chordates (Perciformes and Scorpaeniformes such as *Gobius niger*, *Gobiusculus flavescens*, *Pholis gunnellus*, *Pomatoschistus* spp., and *Myoxocephalus scorpius*).

Similarly, previous studies have found that abundance and biomass of grazing species like the periwinkles *Littorina* spp. increase among oysters and that the genus has a preference for oyster and mussel reefs (Kochmann et al. 2008, Markert et al. 2010). Moreover, decapods like shore crab (*C. maenas*) and rock shrimp (*P. elegans*) have also been found to be more closely associated with bivalve beds (where they find refuge and food) compared to sand flats (Posey et al. 1999, Tolley & Volety 2005, Norling & Kautsky 2007, Kochmann et al. 2008).

In this study, the effects of the blue mussel shell treatment were often found to resemble the control treatment. This may be an effect of the blue mussel shell treatment being the bivalve treatment with the least structural complexity, as the blue mussel shells in some plots were dispersed by waves to outside of the plots, and also fell apart during the experimental time frame. Significant differences in epibenthic fauna species richness, abundance and biomass was, however, observed between the control and blue mussel shell treatments, indicating that the coverage of mussel shells was still high enough to produce realistic results (although the importance of the habitat may have been underestimated in this study).

Autogenic engineering effects on epibenthic fauna: comparisons between bivalve treatments

In addition to the observed differences between the bivalve and the control treatments, differences between the shell treatments were also found. Shells of the Pacific oysters had stronger autogenic engineering effects compared to shells of blue mussels, and in some aspects even more than live bivalves. The biomass of epibenthic fauna was higher in the oyster shell treatment compared to the live bivalve treatments, and was lowest in the mussel shell treatment. The differences between shell and live bivalve treatments may be explained by the biogenic habitat that is created by aggregating bivalves like oysters and mussels. Pacific oysters and blue mussels give rise to physical structures with different heterogeneity due to their different size, shapes and living position. The oyster shell is larger, flatter and lies flat on the sea floor or partly buried in the sediment, compared to the smaller blue mussel shell that often has a more erect posture. The spatial arrangement of these aggregating bivalves increases heterogeneity by adding surfaces and space between the shells. In addition, empty oyster shells increase the heterogeneity and available space even more than the mus-

sels by being bigger, thus having an increased surface area and shell volume, and by being more robust and solidly built, providing a new microhabitat for associated species.

Despite the higher biomass in oyster shell structures compared to the live bivalve treatments, and live bivalve treatments compared to the mussel shell treatment, abundance of the epibenthic fauna was not affected by the treatments. This pattern of increased biomass but unaffected abundance indicates a preference for the oyster shell and live bivalve treatments of larger organisms, and for the mussel shell treatment by smaller-sized individuals. This is probably due to the difference in shell volume and aperture width between oysters and mussels, imposing limits to the size of colonizing organisms in habitats with small shelters (Gutiérrez et al. 2003). The oysters have more curved shell shape, rough shell structure and larger shell volume and aperture width than mussels, which offer different type and size of habitat resources to the associated species. Supporting this hypothesis, while the mussel shell treatment was dominated by small crustaceans such as Corophiidae sp., *Idothea* sp., *Jaera* sp. and Gammaridae/Talitridae/Aoridae, and also by *M. edulis* juveniles, the oyster shell and live bivalve treatments favoured some fish species such as *G. niger*, *G. flavescens* and *Pomatoschistus* sp., and some decapods (*Macropodia rostrata* and *Galathea* sp.). These results are supported by previous studies, which have shown that there are significant differences in invertebrate community structure between these bivalve communities (Kochmann et al. 2008, Markert et al. 2010).

Furthermore, despite the observed differences in the physical structures of live bivalves, no differences in the epibenthic and infauna communities in treatments with live oysters or blue mussels were found in this study, indicating a similar autogenic contribution to the habitat from both bivalve species. In contrast, Markert et al. (2010) found twice as high total mean abundance and total biomass in *C. gigas* patches as in *M. edulis* patches. The varying results may be a consequence of different treatments being applied in our study and the study performed by Markert et al. (2010). In this study, only solitary oysters, lying flat on the sandy bottom, were used, while the study performed by Markert et al. (2010) was performed using an oyster reef-structure as habitat, with *M. edulis* present at the same abundance as in the *M. edulis* patches treatment. This indicates that the response of the epibenthic fauna community to altered habitat conditions may be density-dependent, as also reported by Green & Crowe (2013).

Autogenic engineering effects on fish fauna

Empty shells of Pacific oysters and live bivalves were shown to have positive effects on the fish assembly. At the southern site, the fish species richness, abundance and total biomass were highest in the oyster shell treatment and lowest in the control and mussel shell treatments, with the oyster and blue mussel treatments in between. These results are in line with previous studies, which show that the oyster reefs support both stationary and transient fish species (Breitburg 1999, Posey et al. 1999, Tolley & Volety 2005).

Furthermore, previous studies show that oyster and mussel habitats support a wide variety of fishes (Jansson et al. 1985, Breitburg 1999, Posey et al. 1999, Tolley & Volety 2005). The most abundant fish species are small benthic species like gobies that are important in the estuarine food web. These fish are dependent on oyster and mussel beds to varying degrees for feeding, reproduction and shelter from predators. Among the most dependent are the small resident fishes like the black goby (*G. niger*), that attach their eggs to unfouled, articulated oyster shells, and the sand goby (*Pomatoschistus minutus*), that often uses a mussel shell half as a roof for its nest (Crabtree & Middaugh 1982). Although not significant, a similar preference for blue mussel shells by *Pomatoschistus* spp. and for oyster shells by *G. niger* was observed in this study. Furthermore, previous studies from the Baltic Sea support that *M. edulis* bottoms offer good shelter for the black goby (*G. niger*), eelpout (*Zoarces viviparus*) and butterfish (*P. gunnellus*) (Jansson et al. 1985). Supporting this result, *P. gunnellus* preferred mussels and oyster shells in this study. Furthermore, *M. scorpius* demonstrated a strong preference for oyster shells, with a 10-fold increase in average abundance, and even more for the biomass, compared to the control treatment, although other shell environments were also beneficial for the species. As discussed previously, the large gapes of the oyster shells provide nesting sites and hiding places for larger fish species, which may explain the preference of *M. scorpius* to this habitat. The species *G. flavescens* also displayed distinct habitat preferences, as it was only present in blue mussel and oyster shell treatments.

Habitat preferences of different fish species may be related to their body shape. For example, *M. scorpius* (quite large with a large head) had a clear preference for the oyster shell habitat, while *P. gunnellus* (very slim body shape) demonstrated an equally large preference for the blue mussel habitat (where it

could utilize the relatively small crevices created by the blue mussel clusters). In addition to the resident fishes, both oysters and mussels are extensively utilised by more widely ranging fish species. In the present study, a total of 12 fish species were found; enhancing heterogeneity and topographical relief within mussel beds (by adding oyster reef structures) may attract more fish species. Furthermore, we observed large differences in fish species dominance among bivalve shell treatments. Winter-induced mass mortalities of the 2 bivalve species (e.g. post-winter 2009/2010, Strand et al. 2012) may increase the occurrence of shell habitats. An increase of Pacific oysters in shallow areas along the Swedish west coast may thus increase the occurrence of fish species such as *G. niger*, *M. scorpius*, *P. gunnellus* and *G. flavescens*. Increasing the abundance of predatory fish in the system may change the balance of the food web. For example, it may have negative effects on the mesograzers in the system (increasing filamentous algae), but may at the same time increase the food source for top predators (birds and other fish) within the food web. As shells of Pacific oysters are a new structure introduced into the Swedish ecosystem only a few years ago, we expect large effects on the fish assemblage to occur.

CONCLUSIONS

In this study, Pacific oysters and blue mussels demonstrated strong ecosystem engineering effects on associated epibenthic fauna (including fish) in subtidal sandy habitats by increasing abundance and biomass of associated species in bivalve beds and shell structures compared to bare sediment. This indicates that large changes in the epibenthic fauna community may occur if the Pacific oysters continue to establish more populations, as predicted for the region. The live and post-mortem shell structures of these 2 bivalves also demonstrated different structuring effects on the associated community, but no major differences in epibenthic fauna community structure between treatments with live bivalves were documented. Furthermore, post-mortem shell structures of Pacific oysters were found to have even stronger structuring effects than live bivalves in some cases. We documented changes occurring at lower densities (i.e. solitary oysters) compared to previous studies. However, Pacific oysters can produce more solid structures (even reef formation), a habitat structure that is not only new to the region but that has also been proven to have large effects on the

epibenthic community in other regions. Thus, as oyster reef formation in Sweden is increasing, the effects on the native community structure can be expected to be even greater compared to that documented in this study. In addition, as harsh winters may lead to high oyster mortalities, the availability of post-mortem shell structures alone can cause significant changes to the ecosystem. In conclusion, based on the results presented in this study, we predict that large changes in native assemblages of epibenthic fauna and fish will occur as the establishment of the Pacific oyster continues in Sweden.

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